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INTERTIDAL PLANT AND ANIMAL ZONATION IN THE VICINITY OF NEAH BAY, WASHINGTON

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Cape Flattery, a rocky headland with cliffs over one hundred feet high, at the southern side of the entrance to Juan de Fuca Strait, is the extreme northwestern point of the continental United States (fig. 1). Three-eighths of a mile off shore is Tatoosh Island, a mass of rock about a quarter of a mile in diameter, partly encircled by reefs but with a sandy beach favorable for landing in a dory. Five miles inside the Cape lies Neah Bay, a small and, until the recent construction of a long breakwater, a rather open harbor, with an Indian village on its southern shore. The northeastern side of the bay is formed by Waadah Island, a narrow strip of land well wooded but with precipitous rocky shores. About two miles eastward from Waadah Island are Seal Rock and Sail Rock (fig. 2), two prominent landmarks of unusual appearance, one-quarter of a mile apart and less than half a mile off shore.

Remote and little visited by scientific workers, the region is characterized by rugged, surf-beaten shores, large tidal range, strong tidal currents, cold water, heavy rainfall, cool air, a low percentage of sunshine, and considerable fog. With the exception of occasional sandy beaches, the shores are rocky and usually steep, and reefs exposed to heavy surf are numerous. In a few places there are wide, wave-cut benches of rock, either well within the littoral zone or awash at high tide. Some of these are so completely covered with large slippery brown algae that the footing is very precarious, and they are commonly strewn with large boulders, some exposed and some awash, so that it is difficult either to wade over the flats or to go among the boulders in a dory. Some of those on Seal Rock, however, are free of boulders and large algae and offer good footing.

As a biological environment the region is exceptionally interesting. A deep and narrow submarine canyon cuts across the continental shelf from the southwest, shoaling gradually in such a way as to bring into the Strait a mass of cold bottom water, rendering the surface temperatures at the entrance definitely colder in summer than those of regions immediately to the north and south along the adjacent coast, and contributing to a rather unusual thermal equability throughout the year. While few temperature records are available from Neah Bay itself, monthly records covering a period of about five years have been obtained from the middle of the Strait, off Pillar Point, about twenty miles to the eastward. These were taken on the scientific cruises of the motorship *Catalyst*. The minimum surface temperature recorded during a five-year period was 5.85°C and the maximum 13.29°C, the latter figure being obtained on an ebb tide in August. During the year 1938 the total range was from a minimum of 7.70°C on February 12 to a maximum of 10.74°C on August 8, constituting a variation of only 3.04°C for the entire year. Conditions at Neah Bay may be expected to be even more stable than those at the point where these temperatures were taken.

Air temperatures, while of course more variable than those of the water, tend likewise to avoid extremes, so that organisms occupying the intertidal zone dwell in a remarkably constant thermal environment.

The heavy rainfall (ranging from 79.75 to 136.16 inches a year, with an average of 109.24 inches for a 17-year period) might be thought of in one sense as a condition of environmental stress. Undoubtedly organisms in the intertidal zone will be subjected to difficulties if exposed to frequent downpours when the tide is out unless they possess some mechanism for adjustment to osmotic changes. For most intertidal forms, however, desiccation in warm sunshine is a greater hazard, so that in general the heavy rainfall over the area may be regarded as a favorable environmental factor in this connection.

Most impressive of all to the student of littoral ecology, the large daily tidal range (exceeding 10 feet on the greatest tides) combines with the unusual features of the shore line to produce conditions favorable to a definite stratification of plant and animal life in the intertidal zone. While it is a commonplace of seashore biology that different communities will be found at different levels between high and low tides, in regions where the tidal range is small or the shores are gently shelving the limits of the vertical distribution

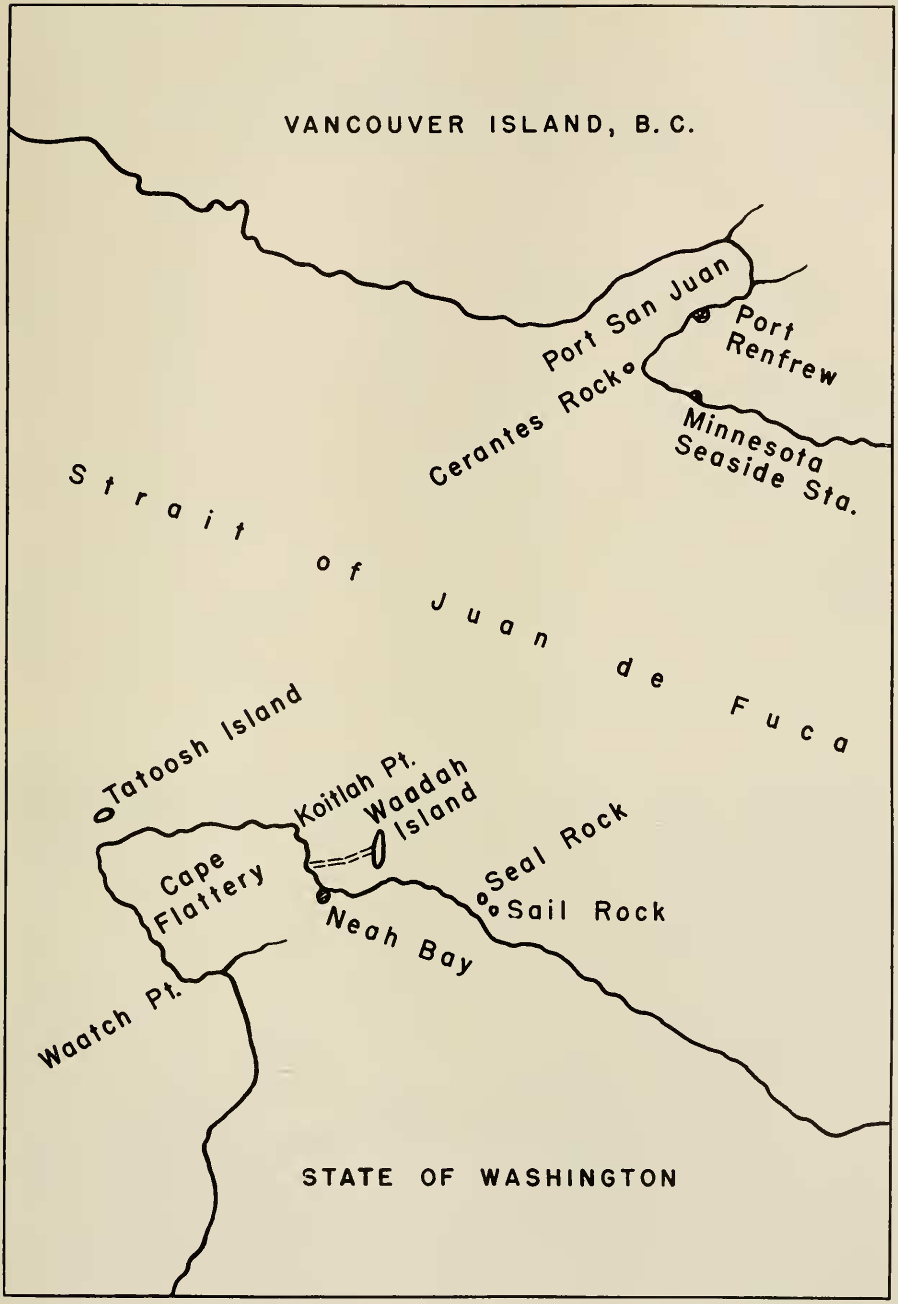

Fig. 1. Map of Neah Bay and vicinity. Dotted line indicates new breakwater.

of a given biome are not easily established. In the vicinity of Neah Bay, each wave-cut bench presents a biological picture characteristic of the level at which it occurs, and on the steep rock walls which are so prevalent the distribution of the dominant organisms takes the form of horizontal bands laid out with almost diagrammatic exactness (figs. 3 and 8).

Localities Investigated

Waadah Island, which is about half a mile long and 220 yards wide, forms the northeastern side of Neah Bay. It bears a coniferous forest with a dense undergrowth of shrubs. The east shore is subject to heavy surf especially in easterly winds and at outgoing tides. The northern end is especially swept by tides and beaten by surf. The east side of the north end, later referred to as Postelsia Point, is subject to heavy waves and surf not only at outgoing tides, which hit it directly, but also at incoming tides which swirl around it. The water at the southwest side of this island is very shallow and numerous large rocks are exposed or awash at low tide. Reefs are numerous. One extends from the southwest corner of the island, and another extends eastward from the central portion of the east side. There is no sandy beach on Waadah Island but landing is readily made on a somewhat rocky beach at the southwest end at slack water in good weather. Frequent landings have also been made at other points when conditions were favorable.

Fig. 2. Seal Rock, with Sail Rock at extreme right, and adjacent mainland.

Seal Rock is about 100 feet high and has vegetation on its upper portion, which is composed of tilted strata of sandstone similar to those of Waadah Island. It lies about 2 miles southeast of Waadah Island and about 660 yards off shore. From certain points the appearance of this rock suggests that of a giant seal (fig. 2). Sail Rock is near Seal Rock. There is no beach on either of these islands, but landing is easily made on the rocks on the south side of Seal Rock at low tide under favorable conditions. Strong tides, both incoming and outgoing, sweep past this rock on both the north side and the south side. The incoming tides beat directly upon the west end of the rock and swirl around the east end, while at outgoing tides the east end gets the beating and the west end gets the swirl.

An interesting feature is the rocky ledge or platform forming the base of Seal Rock. This forms a shelf all around the rock, widest on the east end, approaching the horizontal, then falling off rather steeply at the edges. It is exposed at low tide, and covered at high tide by shallow, churning water.

A dory was landed on this ledge at the north side in calm weather at a 7.6 foot tide and the depth of the water was noted during 20 successive waves. At most of these the depth of the water was about 18 inches and at some of them it was about 30 inches. Between waves there was about 6 inches of water on the ledge.

The occurrence of the two large kelps, *Nereocystis* and *Macrocystis,* was studied by one of us (Rigg) several years ago during two summer visits in 1911 and 1912 and some general observations were made on other algae. During the first of these a trip was made from Neah Bay to Tatoosh Island in a dug-out canoe with an Indian companion. The second trip was made from Seattle to Neah Bay in a 40-foot launch, and permitted examination of much of the American shore of Juan de Fuca Strait. In 1933 a trip was made at low tide in calm weather, in a skiff powered with an outboard motor, along the rocky shore from Neah Bay almost to Cape Flattery, and landings were made at several places.

Most of the detailed study of the region was made during the summers of 1936, 1937, and 1938. These trips were made in the research motorship *Catalyst* from the Oceanographic Laboratories of the University of Washington during the course of the summer work at Friday Harbor. The trips were made in July and on each trip Waadah Island was visited at one early morning low tide and Seal Rock on the following morning. Trips which permitted observations at only one low tide had been made on the *Catalyst* during the summers of 1933 and 1934, but considerable time was spent on these trips in finding the most desirable points for study and the most advantageous places to land from the dories in order to reach them. A trip to Port San Juan and vicinity on Vancouver Island, B. C., was made June 29 to July 1, 1939, and studies were made of the conditions there for comparison with those at Neah Bay. In August, 1948, one of us (Miller) revisited Neah Bay to

Fig. 3. "Postelsia Point" on Waadah Island, showing zonation of algae. 1. Ralfsia-Prasiola. 2. Endocladia-Gigartina. 3. Postelsia. 4. Halosaccion. 5. Alaria. 6. Lessoniopsis. Laminaria and Nereocystis zones are farther seaward and not shown here.

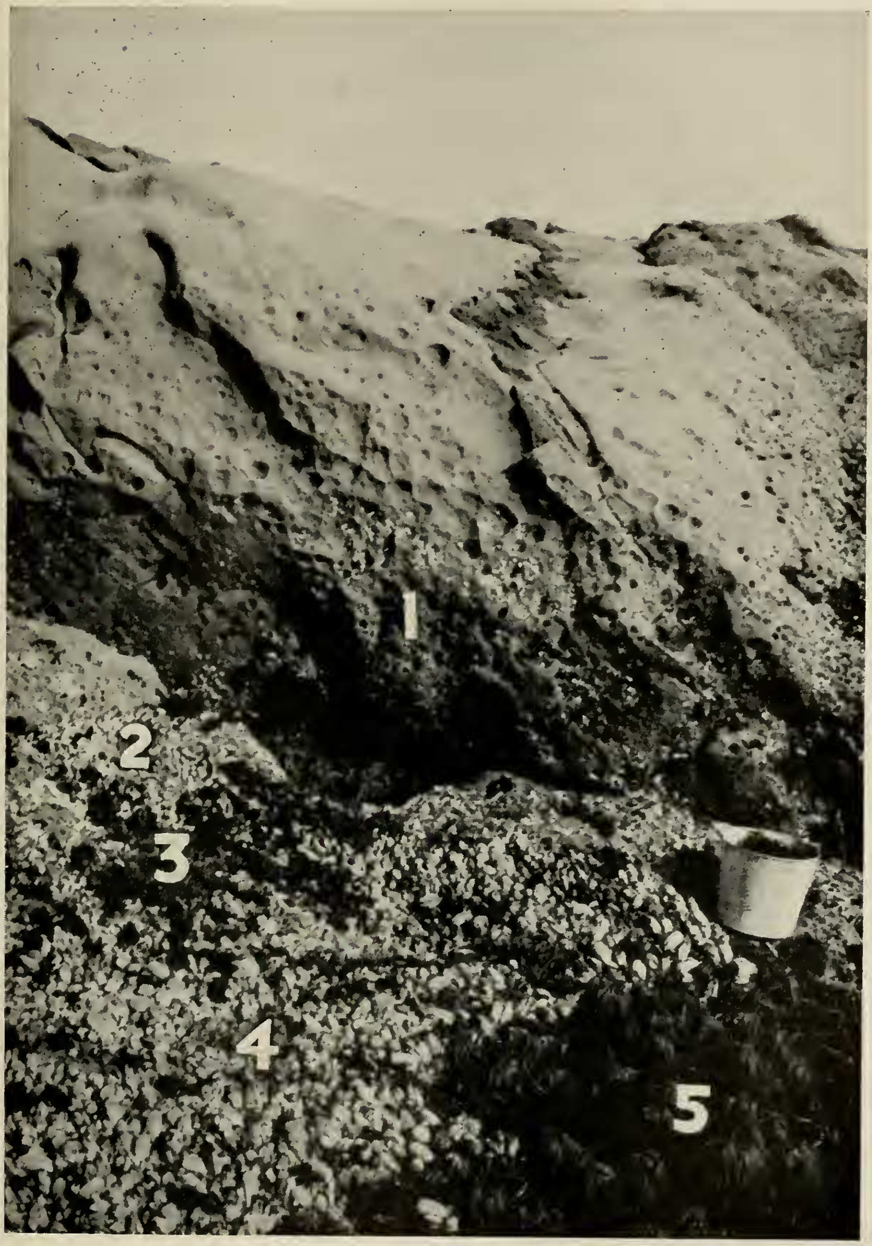

Fig. 4. Detail near upper left of figure 3, showing upper intertidal and splash zones. 1. The dark discoloration is *Ralfsia verrucosa,* the small scattered clumps are *Prasiola meridionalis,* and the white spots scattered *Balanus glandula.* 2. Dense stand of *B. glandula.* 3. *Gigartina* sp., intermingled with *Endocladia muricata.* 4. Dense stand of *Mytilus californianus.* 5. *Postelsia palmaeformis.*

observe what changes might have resulted from construction of the new breakwater erected between Waadah Island and the mainland in 1942-43.

The number of persons taking part in the study on each trip during 1936 to 1938 varied from five to ten, and in the course of the three trips included a considerable number of individuals. The writers wish to express their thanks to all who participated. A complete list would be impossible, but special mention should be made of the assistance of Dora P. Henry, Malcolm Miller, Marian Pettibone, L. D. Phifer, Marjorie Poole, R. H. Tschudy, and R. H. Williams.

The Plants and Their Zonation

The five places studied in most detail are: (1) the steep rocky shore of tilted sandstone strata on the east side of the north end of Waadah Island which in this paper is called for convenience Postelsia Point; (2) the narrow surge-washed channels between the parallel reefs of solid sandstone extending several hundred feet northward from the north end of Waadah Island, which in this paper are called for convenience Reef Channels; (3) the flat shore mainly of solid rock and boulders on the southwest shore of Waadah Island; (4) the steep shore of solid rock and the tide-washed ledge above it at the north side of Seal Rock; and (5) the rocks and tide-washed ledge on the south side of Seal Rock. Observations on Sail Rock were made from a dory. Some attention was also given to the entire eastern shore of Waadah Island and the entire shore of Seal Rock.

Brown, red, and green algae are abundant in the region and there are two seed plants, *Zostera marina* and *Phyllospadix Scouleri*. The list of 88 species of algae with the vertical distribution of each for the points at which it was determined in feet above or below the zero tide datum is given in Table I. The conditions under which field work must be done in this region made exact measurements impossible and the data given must be regarded as approximations. Where blanks occur they mean that the presence of the species was not recorded at that point. It is not to be supposed either that the total list or the occurrence of all the species at all the points is complete, and no doubt future studies will add to the list. A schematic presentation of the vertical distribution of the algae at two of the five points studied is given in figures 5 and 6. Their zonation at each of these points is evident. It seems best to discuss the zones at Postelsia Point in some detail and then to compare the zonation at the other points with this one.

Postelsia Point. Eight zones are here clearly distinguished. These in order from top to bottom are: (1) Ralfsia-Prasiola, (2) Endocladia-Gigartina (3) Postelsia, (4) Halosaccion, (5) Alaria, (6) Lessoniopsis, (7) Laminaria, and (8) Nereocystis.

TABLE I
Vertical Distribution of Algae at Selected Localities in the Neah Bay Region

	Tidal levels between which alga is attached				
	Waadah Island			Seal Rock	
A. BROWN ALGAE	Point	Channels	Flat	North	South
1. *Alaria tenuifolia*	1 to 3	0 to 4	0 to 4	0 to 3	0 to 4
2. *Chordaria abietina*					2 to 3
3. *Colpomenia sinuosa*			3 to 5		
4. *Costaria costata*	—1 to 1			—1 to 1	0 to 2
5. *Cymathere triplicata*					—1 to 1
6. *Desmarestia munda*	—2 to 1				
7. *Egregia Menziesii*	—3 to 4	0 to 5	0 to 4	0 to 2	—2 to 2
8. *Fucus evanescens*		7 to 9			
9. *Fucus furcatus*		7 to 9	7 to 9	8 to 9	5 to 9
10. *Hedophyllum sessile*			0 to 3	0 to 5	—1 to 3
11. *Laminaria Andersonii*	—3 to 2	0 to 3	0 to 6	—3 to 1	—1 to 6
12. *Leathesia difformis*					4 to 6
13. *Lessoniopsis littoralis*	—2 to 2			—3 to 3	—2 to 2
14. *Macrocystis pyrifera*					—2 to 1
15. *Nereocystis Luetkeana*	—10 to 1			—10 to 4	—10 to 0
16. *Pleurophycus Gardneri*	2 to 0			—1 to 0	—1 to 2
17. *Postelsia palmaeformis*	5 to 7				
18. *Pterygophora californica*					—4 to 1
19. *Ralfsia verrucosa*	9 to 13			8 to 10	7 to 9
20. *Soranthera ulvoidea*					2 to 3
B. RED ALGAE					
1. *Agardhiella coulteri*			Drift		
2. *Amphiroa tuberculosa*	1 to 3	0 to 8	0 to 6	—2 to 8	0 to 7
3. *Anatheca furcata*	—1 to 0	—1 to 0			
4. *Bangia fuscopurpurea*	4 to 6				1 to 5
5. *Callithamnion Pikeanum*	—2 to 2				
6. *Callophyllis crenulata*		—1 to 2			
7. *Callophyllis edentata*		—2 to 1			
8. *Callophyllis flabellulata*		—2 to 1			
9. *Callophyllis heanophylla*		—2 to 1			
10. *Ceramium californicum*		0 to 3			
11. *Ceramium pacificum*			2 to 6		
12. *Ceramium washingtoniense*		5			
13. *Constantinea subulifera*		1			2 to 4
14. *Corallina officinalis*	—1 to 6	0 to 2		0 to 5	4 to 6
15. *Cryptopleura Ruprechtiana*		—1 to 1			
16. *Dasyopsis plumosa*	—2 to 1	—1 to 1			
17. *Endocladia muricata*	7 to 9	7 to 9		6 to 8	
18. *Fauchea Fryeana*	—2 to 4	0 to 2	0 to 2	—2 to 2	—2 to 3
19. *Gigartina exasperata*			3		6
20. *Gigartina leptorynchos*	4 to 6	[500 ft. S. of point]			
21. *Gigartina papillata*		4 to 8	5 to 8	6 to 8	5 to 8
22. *Gigartina* sp.	7 to 9				
23. *Gloiopeltis furcata*		9	8 to 9	8 to 9	7 to 9

	Tidal levels between which alga is attached: Waadah Island			Seal Rock	
	Point	Channels	Flat	North	South
24. *Gloiosiphonia californica*		—1 to 1			
25. *Grateloupia Cutleriae*		—1 to 1			
26. *Griffithsia pacifica*			Drift		
27. *Halosaccion glandiforme*	3 to 9	6 to 9	5 to 7	7 to 8	5 to 7
28. *Heteronema boreale*		—2 to 0			
29. *Hildenbrandtia rosea*		0 to 3	0 to 3	0 to 3	0 to 3
30. *Hymenena flabelligera*	—2 to 1	—1 to 1		0 to 3	—1 to 1
31. *Iridophycus flaccidum*	—1 to 1	0 to 2		0 to 3	—1 to 1
32. *Laurencia spectabilis*		0 to 1			
33. *Lithothamnion* sp.	—2 to 5		6	—2 to 3	0 to 4
34. *Membranoptera alata*		—1 to 1			
35. *Microcladia Coulteri*	1 to 3	6	2 to 6	7	2 to 7
36. *Nitophyllum mirabile*		0 to 1		2	1
37. *Odonthalia dentata*		2 to 5			
38. *Odonthalia floccosa*	4 to 6	0 to 2			0 to 5
39. *Opuntiella californica*	—1 to 1			—1 to 1	
40. *Platythamnion pectinatum*		—2 to 1			
41. *Plocamium pacificum*	1 to 3	5		4 to 6	6
42. *Polyneura latissima*		—2 to 1			
43. *Polysiphonia senticulosa*		—2 to 0			
44. *Polysiphonia tenuistriata*			—2 to 1	—1 to 1	1 to 3
45. *Polysiphonia urceolata*				—2 to 1	
46. *Porphyra naiadum*			0 to 3		
47. *Porphyra perforata*			0 to 6	8 to 9	3 to 6
48. *Prionitis Lyallii*		8 to 9	8 to 9	8 to 9	5 to 7
49. *Pterosiphonia dendroidea*			Drift		
50. *Ptilota tenuis*	—2 to 1	4 to 5			
51. *Rhodochorton penicilliforme*		1 to 3			
52. *Rhodomela larix*	4 to 6			7 to 8	3 to 7
53. *Rhodymenia palmata*	—1 to 0				
54. *Turnerella pacifica*		—1 to 1	—1 to 2	—1 to 1	—1 to 2

C. Green Algae

	Point	Channels	Flat	North	South
1. *Chaetomorpha cannabina*		Tide pools			
2. *Cladophora glaucescens*		Tide pools			
3. *Cladophora Stimpsonii*			1 to 3		
4. *Cladophora trichotoma*			7 to 8		4
5. *Codium adherens*		0 to 2	1 to 3		
6. *Codium fragile*			2 to 4		1 to 5
7. *Enteromorpha intestinalis*		Tide pools			
8. *Enteromorpha tubulosa*		Tide pools			
9. *Gomontia polyrhiza*		Tide pools			
10. *Prasiola meridionalis*	10 to 12				10 to 12
11. *Spongomorpha coalita*	1 to 3		1 to 3		1 to 3
12. *Ulva californica*	8 to 9		6	8 to 9	
13. *Ulva lactuca*			—3 to 4		—3 to 0
14. *Ulva linsa*		Tide pools			

The upper zone consisting exclusively of two species, *Ralfsia verrucosa* and *Prasiola meridionalis,* extends from the nine foot level to more than a foot above extreme high tide where it is wetted, so far as sea water is concerned, only by waves and spray. On many days in both summer and winter this entire zone is exposed even at high tide. *Ralfsia,* whose individuals consist merely of an incrustation on the rocks with no evident free portions, seems well fitted for such an existence, while *Prasiola,* often in crevices, and always with its minute individuals so matted together that water is always held within the mat and the surfaces are thus never dry, successfully maintains its existence up to within a foot of the upper limit of its only companion in the zone.

An unidentified species of *Gigartina,* intermingled with *Endocladia muricata,* grows in irregular patches just below the Ralfsia-Prasiola zone.

The Postelsia zone extends through a vertical distance of a little over 2 feet. Its characteristic plant, *Postelsia palmaeformis,* has a striking appearance. Its erect, flexible, hollow stipe, one to two feet tall, bears a dense cluster of narrow, tapering fronds at its top and clings to the rock by a massive holdfast. This Point was observed at a 7.7 foot tide and it was found that the waves were just running over the tops of the plants. The stipe bends as the waves strike it and recovers its erect position as the water recedes, as if made of rubber. Its appearance when exposed at low tide or when hammered by

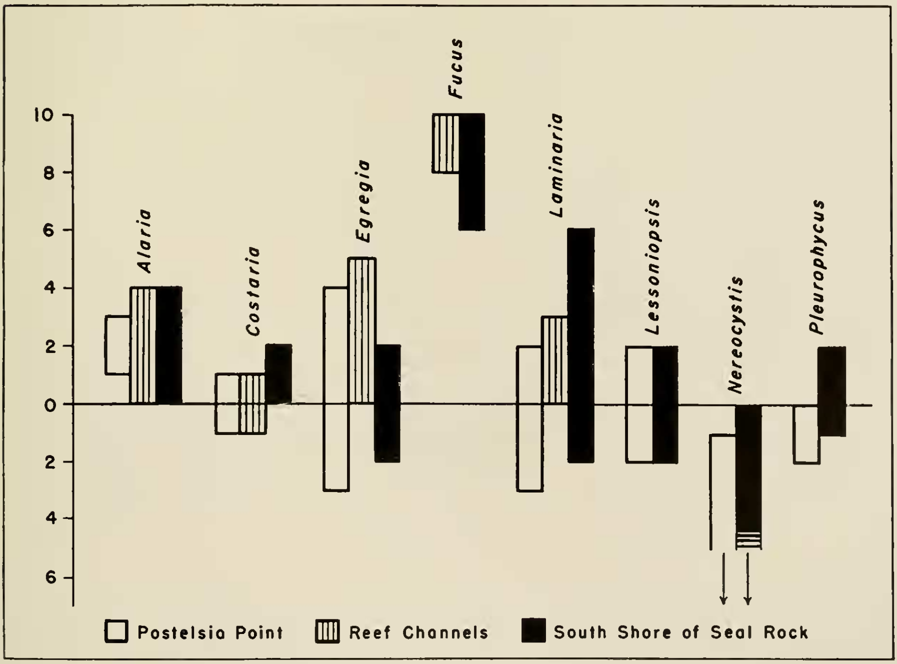

Fig. 5. Chart showing vertical distribution (in feet above or below the zero tide datum) of the principal brown algae at three localities in the vicinity of Neah Bay. *Postelsia,* occurring only at Postelsia Point, is omitted from the chart.

waves well justifies its common name, sea palm. This plant is not found at any of the other four points studied (Table I), but is abundant at the eastern end of the reef extending eastward from the east side of Waadah Island and has also been seen on Cape Flattery and the neighboring rocks and on Tatoosh Island. It occurs also on the exposed rocky shores in the vicinity of Port Renfrew on Vancouver Island, B. C. It is abundant there at the site of the old Minnesota Seaside Station and also on Cerantes Rock. In all these places its vertical distribution seems to be approximately the same as at Postelsia Point. It seems, so far as seen, to flourish in this region only on steep solid rock shores where wave action is violent. On a rock near Cerantes Rock, however, practically all the *Postelsia* found was growing on mussels and barnacles. The rocky surface was so completely covered with the animals that there was no place else for the plants to attach themselves.

Extending into this zone from below are *Odonthalia* and *Rhodomela* whose tough, flexible stipes are bent by waves suddenly and forcibly in every direction from their holdfasts without breaking and whose numerous short matted branches hold water in the mat when exposed and furnish a cushion which softens the violence of contact with rocks when their distal portions are thrown about by the waves. *Halosaccion glandiforme* which extends entirely through the Postelsia zone will be discussed in connection with the next zone below. *Gigartina leptorynchos* does not occur with *Postelsia* but is at the same level on flat rocks a short distance south of Postelsia Point. Its long, narrow, tubular thallus with its numerous short proliferations lies flat upon the rock at low tide. Its anchorage is firm and its adaptation to its habitat is analogous to that of *Odonthalia* and *Rhodomela* and seems even more perfect. It looks like a tough customer which, in the slang of the day, "can take it." The only specimens of *Bangia fuscopurpurea* identified at this point occurred on *Gigartina leptorynchos,* taking advantage of the protection offered by this hardy plant.

The Halosaccion zone, as a distinct zone, is the narrowest of all, extending through a vertical distance of only one and a half feet (3 to 4.5). Its dominant plant, *H. glandiforme,* extends also through the Postelsia zone and nearly to the top of the Endocladia-Gigartina zone, but its dominance at the lower level is clearly evident though the encrusting *Lithothamnion* and the small calcareous *Corallina officinalis* in varying abundance extend entirely through the zone. *Fauchea Fryeana* occurs sparingly in its lower portion and *Odonthalia* and *Rhodomela* extend from above into its upper portion. *Halosaccion glandiforme* is somewhat like a small balloon a few inches long, less than an inch wide, and anchored at one end. Many of the individuals when collected at low tide contain so much water that it can, by slight pressure, be forced out in fine streams in various directions through small pores near the distal end. This internal water seems to take care of the desiccation problem and the dense growth of individuals in this location furnishes mutual protection against mechanical injury by wave action.

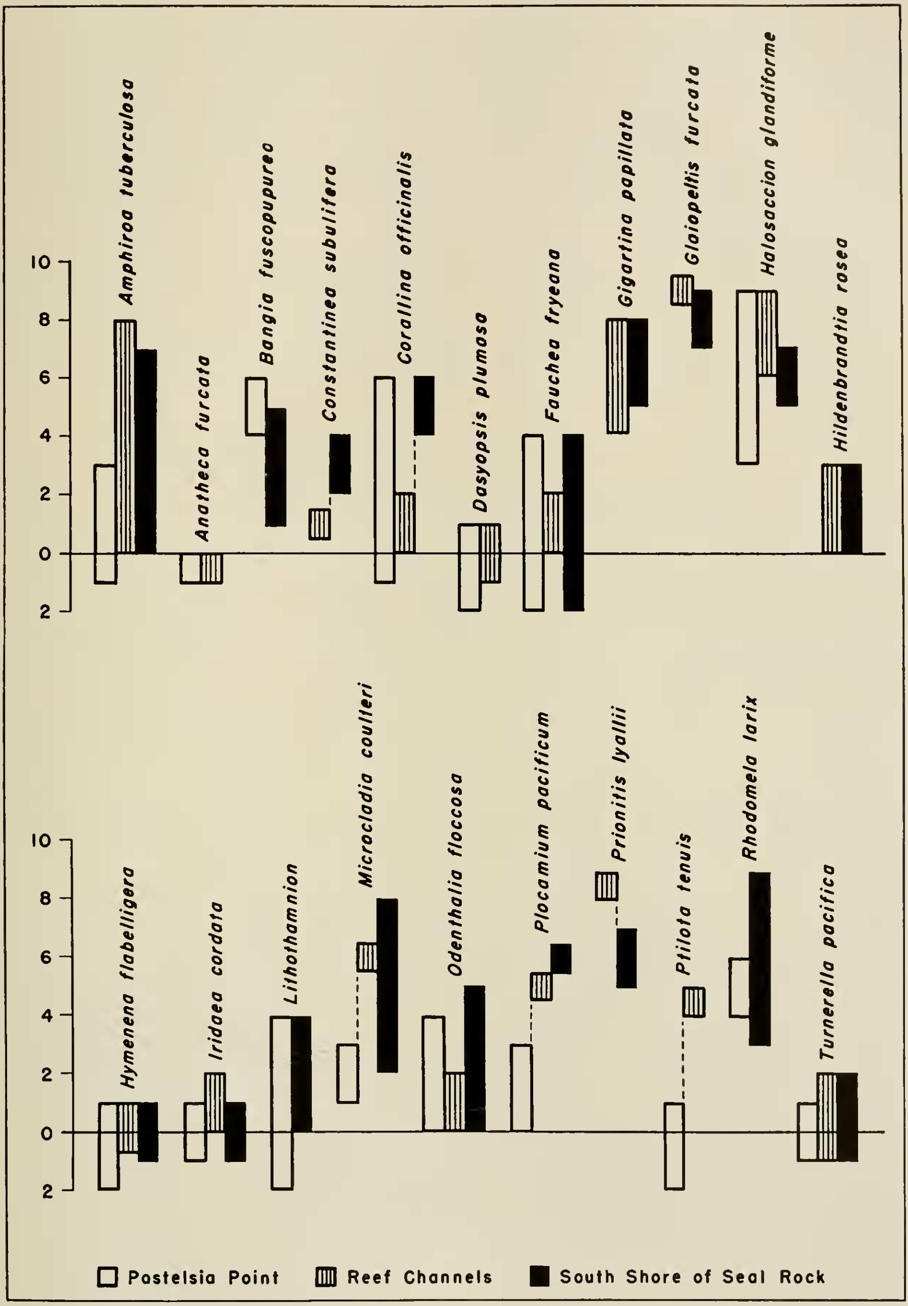

FIG. 6. Chart showing vertical distribution (in feet above or below the zero tide datum) of the principal red algae at three localities in the vicinity of Neah Bay.

The Alaria zone is also narrow, extending in vertical distance only from the one-foot to the three-foot level. It is clearly dominated by *Alaria tenuifolia* which is the only species of large individuals abundant in it. It is limited to this zone as are also the small individuals of *Microcladia, Plocamium,* and *Spongomorpha.* Enormous individuals of *Egregia Menziesii* occur occasionally throughout this zone but this species will be discussed in connection with the next zone below. *Fauchea Fryeana,* which in the region of the San Juan Islands is mostly dredged at 6 to 8 fathoms, here occurs in the littoral zone. *Spongomorpha coalita,* with its filaments held together by small hook-like branches so that they form a dense strand, seems well fitted to withstand mechanical injury and desiccation. The crustaceous *Lithothamnion* and the small stiff calcareous individuals of *Amphiroa* and *Corallina* flourish well in this zone.

The distal portion of the fronds of *Alaria* are worn off by the mechanical effect of wave action and occasionally one finds individuals on which the frond has been entirely destroyed so that only the holdfast, stipe, and sporophylls remain. The production of spores thus seems assured though the vegetative portion may be largely sacrificed. It has been found, however (Frye, 1918), that there are annual rings in the stipe of this species and that the midrib continues to grow in length even when the blade at its margins is destroyed. It thus seems possible that the plants of this species may continue to live in spite of rough treatment.

The Lessoniopsis zone is completely dominated by a dense growth of enormous plants of *Lessoniopsis littoralis.* This is a perennial plant with a stout stipe several inches thick at the base and so hard that a small axe is the best tool for securing specimens. The stipe tapers upward and forks repeatedly bearing a long slender frond at the end of each branch. Zoospores are produced in the sori in these fronds. The great weight of this plant and the flexibility of its stipe cause it to hang down at low tide. A single plant held over the shoulder by its stipe and hanging down the back almost to the ground makes a good load for an able bodied man to carry. This species is on exposed rock shores throughout the region and is seen on Seal Rock, Sail Rock, and along the rocky shore from Koitlah Point to Cape Flattery. It furnishes advantageous anchorage on its stipe for numerous red algae, and large masses of a sponge are numerous on it. Among the red algae growing on its stipe or holdfast are *Dasyopsis* and *Callophyllis. Egregia Menziesii* is common in this zone. No plants were measured here but a plant which was collected at False Bay on San Juan Island in July, 1936, may be taken as characteristic of the species. It had 14 stipes from one holdfast. These stipes varied in length from 8 to 25 feet, five of them approximating the maximum length. It required three men to carry it away. Its holdfast is massive and its stipe is like a long strip of leather. The fronds are borne along the edges of the stipe throughout its whole length and are very small with a small float at the base of each. Zoospores are borne in sporophylls among these fronds.

The Laminaria zone extends from —1½ to —3 and is dominated by *Laminaria Andersonii.* It has an erect dark-colored stipe from the tip of which the digitate frond is pendant at low tide. The stems are flexible and are bent by every wave, but constantly return to an erect position. This species extends upward through the Lessoniopsis zone and into the Alaria zone but is dominant only within the limits stated above. *Pleurophycus Gardneri,* a Laminaria-like kelp with a broad midrib in which the zoospores are borne, extends from above into this zone, as do also such red algae as *Dasyopsis, Fauchea, Hymenena,* and *Rhodymenia,* which in the waters among the San Juan Islands are obtained mostly by dredging at depths of 6 to 8 fathoms. The factors in the occurrence of these red algae at higher levels in the Neah Bay region than in the San Juan Island region are not clear. A possible factor is less intense light due to the prevalence of foggy and cloudy weather and protection from direct sunlight by the dense growth of brown algae.

The Nereocystis zone extends from about 3 feet below datum to an undetermined depth. No soundings were made here but our work in the Puget Sound region and Alaska indicates that *Nereocystis* does not commonly grow in water that is much deeper than 10 fathoms. This plant and its relation to its habitat have been discussed in so many papers that it is unnecessary to give details here. (Crandall, 1915; Frye, 1906, 1915; Hartge, 1928; Hurd, 1916, 1917; MacMillan, 1899, 1901; Muenscher, 1915; Rigg, 1912, 1915, 1915a, 1917; Setchell, 1908, 1912; Setchell and Gardner, 1925.) No doubt red algae

Fig. 7. "Reef Channels," north end of Waadah Island.

grow on the stipe and holdfast of this kelp here as they do elsewhere. The plant seen most abundantly on the distal portion of the stipe of this plant in the Neah Bay region is a filamentous diatom (*Navicula* sp.).

Comparisons of zonation. In general there is considerable similarity between the zonation at Postelsia Point and at the other four places studied, but there are also noticeable differences in both the occurrence of species and their vertical distribution. It seems possible to correlate these differences to a certain extent with environmental factors.

The Reef Channels are not exposed directly to tidal currents and not to direct action of waves except in northerly winds but are subjected to heavy surge of water in and out, giving rise to some surf. There is always water in these channels even at extreme low tide and there are many rocks in them either exposed at low water or awash in the waves. Brown algae are abundant in these channels both on the rocks in the bottom and on the steep sandstone walls which border them. The first impression that one gets of these channels at low tide is of a dense growth of brown algae forming a thick tangled layer on the rocks or pendant from the walls. Mixed with the brown of the tangled mat is the vivid green of *Phyllospadix Scouleri* whose rhizomes cling to the rocks while its long slender leaves are swept about in the surge. Among the bases of the leaves mature pistillate flowers in rows two or three inches long on a spadix and safely enclosed in the boat-shaped spathe were commonly found in July. The vigor of the growth of the branching rhizomes suggests that this plant is largely reproduced here vegetatively rather than by the germination of seeds, but no definite information on this point is at hand.

Red algae are more abundant in these channels than they are on Postelsia Point both as to number of species and number of individuals. The greater number of species is apparent in Table I. *Fucus* is also common here. The absence of *Postelsia* and *Lessoniopsis* constitutes a striking difference between the Channels and Postelsia Point. The absence of heavy waves and surf seems to be a large factor in this. The absence of *Ralfsia* and *Prasiola* is no doubt associated with the lack of surf and spray at high levels.

The southwest shore of Waadah Island is more protected than any of the other four places studied. There is no strong tide through the harbor, and the force of westerly and southerly winds is largely broken by the high land across the bay. The force of such waves as do come in is also broken by the large beds of *Nereocystis,* with some *Macrocystis,* which are immediately to the westward. The island itself prevents easterly winds from affecting this shore. The area was visited at a 7.6 foot tide and it was found that the entire rock shore up to the boulders which lie back of it was awash. This shore has fewer algae than any of the other four places. *Ralfsia, Prasiola, Postelsia,* and *Lessoniopsis* are naturally absent. Red algae are, however, numerous both as to species and individuals.

Seal Rock has quite different conditions from Waadah Island as is indicated by the description given earlier in this paper. The strong tides rush past its north and south shores instead of beating directly upon them as at Postelsia Point, while the east and west ends split the seas that strike them directly, and part of their force carries them along the north and south shores. Then, too, the force of surf and spray at higher levels is lessened by their passage across the ledge. *Ralfsia* occurs here, though not at as high a level as at Postelsia Point, while *Prasiola* maintains about the same level as at the Point. *Fucus* is abundant in places but the individual plants are not large.

A notable plant occurring on the south side of this rock but not at the other four places is *Pterygophora californica.* It is mostly in the sublittoral zone, but extends also into the lower littoral as it does also on the neighboring shore of the mainland. It is a stout, erect perennial kelp with annual rings in its stipe. It bears a new crop of fronds at its top each year. Frye (1918) has investigated the age attained by individuals of this species, by means of both annual rings and leaf traces. Those that he examined were from 5 to 13 years old. MacMillan (1902) reports 24 annual rings in a stalk 5 cm. in diameter. A specimen that drifted up on the rocks at False Bay on San Juan Island in July, 1936, had a stipe 6 feet 9 inches tall and had 15 fronds. The considerable number of large plants that had drifted up on the beach at Neah Bay indicates that the plant flourishes abundantly in the vicinity. It was reported by MacMillan (1901) at Port Renfrew on the coast of Vancouver Island opposite Neah Bay. The fact that it drifts up on the west shore of San Juan Island at the inner end of the Strait of Juan de Fuca indicates its abundance somewhere in the Strait. It seems quite possible that these drift plants come from the Neah Bay region or the south end of Vancouver Island. The known facts thus indicate that this plant is abundant in the Neah Bay region but grows mostly so far below low tide that not even its tops are ever exposed. It is occasionally dredged at 6 to 8 fathoms in Peavine Pass in the San Juan Islands.

Small, round shallow tide pools are common in the sandstone at Postelsia Point and other places on the west shore of Waadah Island and also on Seal Rock. The two most important environmental factors for algae which are different in tide pools from those in other places on these rocky shores are (1) that the plants in them are not subject to desiccation, and (2) that the water becomes warmer. The latter is especially true of those that occur in the upper portion of the littoral zone where they are exposed to the sun's rays for several hours at low tide. The plants found in tide pools at the points studied are *Priontis Lyallii, Codium fragile* (with *Ceramium* sp. epiphytic upon it), *Chaetomorpha cannabina, Cladophora glaucescens, Enteromorpha intestinalis,* and *Ulva linsa.* In addition to the algae, *Phyllospadix Scouleri* also occurs in the tide pools on both Waadah Island and Seal Rock. Muenscher (1915) has studied the tide pools of San Juan Island. He quotes data indicating an extreme difference of 5.6°C between the temperatures of the tide pools and that of the neighboring sea water. He lists 8 species of algae in the San Juan tide pools, only one of which

(Prionitis Lyallii) is in our list for the Neah Bay region. He found *Ulva lactuca* while we found *Ulva linsa.* The tide pools of the west coast of Vancouver Island are numerous and striking in character, especially in the vicinity of the old Minnesota Seaside Station. Their origin and general character have been discussed by Henkel (1906). In 1939 we found *Codium fragile* abundant in a large tide pool on Cerantes Rock. The pool was at about the high tide level and was near the middle of the rock. It was under a ledge of rock which gave shade after about 10 A.M. The occurrence of this species in tide pools at high levels in the Neah Bay region and on the west coast of Vancouver Island is in striking contrast with its position in the San Juan Islands, where it occurs at about the —1.0 foot level.

Unusually large tide pools occur on the south side of Seal Rock. These are irregular depressions in the rocky surface of the shale and are not comparable in origin to the small round tide pools in sandstone discussed above. The vegetation of the two types of tide pools also has little in common. A large one at unusually low level contains a wealth of the brown algae which are characteristic of these shores, and in 1938 two *Nereocystis* plants about 8 feet long were growing in it. *Cymathaere triplicata* is abundant in large tide pools at the site of the old Minnesota Seaside Station on Vancouver Island.

The distribution of *Macrocystis* along the south shore of the Strait of Juan de Fuca has been discussed in a previous paper (Rigg, 1913) and the principal beds of *Nereocystis* in the region have been mapped. (Portfolio accompanying Rept. No. 100, U. S. Dept. Agr.) Both of these kelps reach a considerable length (100 feet or more). The size of these and other kelps has been given by Frye, Rigg, and Crandall (1915). It should be emphasized that reports of enormous lengths of several hundred feet previously reported for these kelps have not been verified. These two kelps form considerable beds or "groves" in the Neah Bay region where depth, anchorage and water movement are suitable. The two species intermingle to only a slight extent. Where the two form beds along the shore, the *Nereocystis* is outside and the *Macrocystis* is closer to the shore (Rigg, 1913). *Nereocystis* commonly disappears in winter in the Puget Sound region and in Alaska and it is to be presumed that it does the same in the Neah Bay region. *Macrocystis,* as is well known, is a perennial species with numerous stipes attached to one large holdfast and its growing region is at the distal end. It has a small float at the base of each of its numerous fronds which are scattered along the slender stipe. The sporophylls occur on special short stipes from the holdfast several fathoms under the surface of the water.

Two species of seed plants, *Zostera marina* and *Phyllospadix Scouleri,* occur in the Neah Bay region, and a third one, *Phyllospadix Torreyi,* is found rolled up in considerable quantities on the sandy ocean beaches southward from Waatch Point, though it was not seen growing. The first is a cosmopolitan species whose range on this coast is Alaska to California (Piper, 1906).

It occurs mostly below low tide and its rhizomes grow in sand or mud. The second has already been discussed. Its range is British Columbia to California (Piper, 1906).

Vertical Distribution and Zonation of the Littoral Invertebrates

For the purpose of an initial survey of the littoral invertebrates of the Neah Bay region with reference to their distribution in or proximal to the intertidal belt, four zones were established on the basis of the most obvious ecological factors:

A. *The splash zone,* extending from mean higher high water to the extreme upper limit of occurrence of barnacles or limpets. Approximate limits, +8.0 feet to +14.0 feet (above mean lower low water). Organisms living in this zone are out of water the greater part of the time and must be prepared to resist both rainfall and desiccation, to withstand a wide range of temperatures, and to subsist on intermittent feeding.

B. *The upper intertidal zone.* Approximate limits, +4.0 to +8.0 feet. Organisms in this zone are out of water more than half the time, but are not subjected to the extreme conditions of environmental stress found in the splash zone. They are to some extent sheltered and aided in their resistance to heat and desiccation by the presence of various algae, especially *Fucus, Halosaccion,* and *Gigartina.*

C. *The lower intertidal zone.* Approximate limits, +1.0 to +4.0 feet. Organisms in this zone are exposed by the tide half the time or less, and grow in the shelter of numerous large algae, most conspicuous of which are *Lessoniopsis, Egregia,* and *Alaria* (see figs. 3 and 8).

D. *The demersal zone.* Approximate limits, + 1.0 to —2.0 feet and beyond. This is the zone that is uncovered only at the lowest tides, and while it affords the seashore biologist his best collecting, most of the animals occurring at these levels are not in the ecological sense intertidal forms at all; they are demersal species which at intervals are briefly exposed by the receding tide, an event to them doubtless as unhappy as it is unexpected. Many of the species collected at the lowest tides can also be dredged at depths of 10 to 20 or more fathoms.

For the purpose of comparison with Shelford's (1935) classification of marine biotic communities in the Puget Sound area, the splash zone corresponds with the Littorina-glandula fasciation and the Littorina-cariosus fasciation of the Balanus-M. californianus association of the Balanus-Littorina biome. The upper intertidal corresponds to the Mitella-Mytilus fasciation and the lower intertidal to the Cribina fasciation of the same association. The demersal zone corresponds to the Strongylocentrotus-Pugettia association of the Strongylocentrotus-Argobuccinum biome. This nomenclature is more complex than is required for the present purpose.

Comparison should also be made with the zones which Ricketts and Calvin (1939) have designated (1) uppermost horizon, (2) high tide horizon, (3) mid-tide horizon, and (4) low tide horizon. The major difference is one of nomenclature, the present writers having regarded mid-tide, not as a zone but as the boundary between the upper and lower intertidal regions. A very little vertical displacement would bring the two sets of concepts into harmony. The present authors, either for adequate reasons or from habit, consider that the terminology herein used provides a better picture of the pattern of distribution on a steep rocky shore.

As a matter of fact, all of these concepts are somewhat arbitrary, and to be thought of primarily as categories for convenience of description. There is no sharp dividing line between lower intertidal and demersal, nor between upper and lower intertidal zones. The splash zone is the best defined; nevertheless, its vertical limits vary greatly with immediate local conditions, such as slope of the rock and exposure to wave action or to sun. On the north and northwest sides of Seal Rock, for example, the splash zone extends on the average at least three feet higher than on the east and south; and in a crevice on the northwest side (most exposed to wave action and least exposed to sun) *Balanus glandula* occurs up to 16 feet and *Acmaea digitalis* up to 19.5 feet above mean low water.

At each locality investigated, zones A, B, C, and D were laid out quickly in terms of measurements based on the height of the tide as ascertained from the tide tables, collecting was done as widely as possible in each zone and the specimens were taken to the laboratory for subsequent identification. Notes were also taken in the field of special conditions, peculiarities of distribution, and general impressions gained by the collector. The notes were subsequently correlated with distributions as determined from identified specimens.

In Table II are given the approximate vertical distributions of some sixty organisms as determined in this way. When an organism occurs in two or three zones but has its maximum distribution in one, the zones of lesser distribution are indicated by parentheses. The time available for collecting was so limited that it is reasonable to assume that all of the organisms found are moderately common in the region.

Certain groups are conspicuous by their absence from the table, notably hydroids, nemerteans, annelids, small crustaceans, and Bryozoa. This does not signify that they were absent in the fauna, but only that they were not taken in the course of rapid general collecting. For most of these groups, special attention and special methods are necessary to collect and identify them.

Only three of the five localities of Table I are included in Table II. Not enough collecting was done in the Reef Channels to justify tabulation. The flat on Waddah Island will be discussed separately on a subsequent page.

TABLE II

Vertical Distribution of Littoral Invertebrates in the Neah Bay Region

A=Splash Zone; B=Upper Intertidal; C=Lower Intertidal; D=Demersal Zone

Organisms	Waadah Island Postelsia Point	Seal Rock North Side	Seal Rock South Side
Acmaea cassis		D	D
Acmaea digitalis	A	A	A
Acmaea instabilis		D	D
Acmaea pelta	D		D
Acmaea scutum	C, D	B, C, D	D
Amphissa columbiana	D	C, D	D
Anisodoris nobilis		C	D
Balanus cariosus	B, C	(A), B, C	(A), B, C, (D)
Balanus crenatus	C, D		C, D
Balanus glandula	A, B, (C)	A, B	A, B, (C)
Balanus nubilis	C		D
Balanophylla elegans	D		D
Bittium eschrichtii			D
Cadlina marginata			D
Calliostoma costatum	D	C, D	D
Cancer oregonensis	D		D
Cancer productus			D
Chthamalus dalli		A	A
Crepidula lingulata		C	D
Crepidula perforans		C, D	D
Cribrina xanthogrammica	C, D	D	D
Cryptochiton stelleri			D
Cucumaria chronjhelmi			D
Cucumaria miniata			D
Dermasterias imbricata	D		D
Diodora aspera	D	C, D	D
Entodesma saxicola			D
Evasterias troschelii	D		D
Haliclona cinerea	D	D	
Hemigrapsus nudus	A, B		
Henricia leviuscula	D	C, D	D
Hinnites multirugosus		D	D
Katharina tunicata	D	D	D
Kellia laperousi		D	D
Lepidochitona lineata		C, D	D
Leptasterias aequalis		C, D	D
Littorina scutulata	B		B
Littorina sitchana	A	A	A
Lygida pallasii	A		
Margarites pupillus			D
Mitella polymerus	B	B, C	
Mopalia muscosa		C, D	D
Mytilus californianus	B	B	B
Ophipolis aculeata		C, D	D
Paphia staminea		C, D	D
Petrolisthes eriomerus			D

Organisms	Waadah Island Postelsia Point	Seal Rock North Side	Seal Rock South Side
Pholadidea penita	D	C, D	
Pisaster ochraceus	C, D	C, D	(B), C, D
Pugettia gracilis		D	D
Pugettia productus		C	
Purpura foliata	D	D	D
Rostanga pulchra		D	
Saxicava arctica			D
Saxicava pholadis			D
Searlesia dira			D
Strongylocentrotus drobachiensis	D	D	D
Strongylocentrotus franciscanus	D	D	D
Strongylocentrotus purpuratus	D	C, D	D
Styela montereyensis		D	
Thais lamellosa			D
Thais lima	D	D	
Thais ostrina	B		
Tritonalia interfossa			D
Tritonalia lurida	D	D	D
Velutina laevigata			D

The greatest number of species was found on the south side of Seal Rock, where the relatively sheltered, shelving shore with numerous boulders and an abundance of tide-pools provides the greatest variety of habitats. The steep, surf-beaten rocks at Postelsia Point and on the north side of Seal Rock obviously constitute a more restricted environment. On the other hand, organisms adapted to this rugged life flourish best where pounded by the surf. *Mitella* is noticeably less numerous on the south than on the north side of Seal Rock and *Mytilus,* while abundant at both places, is definitely smaller in the more sheltered location.

Too much significance should not be attached to the presence of an organism at one locality and its apparent absence at another, as additional collecting would be likely to fill the gaps. It is to be remembered that the workers were always driven away from the rocks by the incoming tide before they were ready to go. The vertical distribution shown in the table, however, may be accepted with a greater degree of confidence, especially when the same organism has been found at the same level at two or more places.

The greatest number of species is to be found in the demersal zone. In several cases species that are characteristic of this zone on the south side of Seal Rock extend also into the lower intertidal on the north side. The explanation may well be that the surf on the north side, combined with the greater shade, enables the organisms to live at a higher vertical level without suffering desiccation. A similar difference in the uppermost level of organisms on the north and south sides of the rock has already been noted (p. 342).

In the upper intertidal and splash zones, the number of species is small, but the number of individuals is often very great. In the areas here studied, the bands of sessile or sedentary organisms characteristic of these levels stand out with actually diagrammatic effect. These bands, which are narrow on a vertical wall, spread out on a sloping rock to a width inversely proportional to the declivity (fig. 8).

On the north and east sides of Seal Rock, the wave-cut platform is almost at the level separating zones A and B. Here we find hundreds of square feet covered with a nearly pure stand of *Balanus glandula,* which is invaded about six feet in from the seaward edge by *Mytilus* and *Mitella. Mytilus* also grows in all depressions in the platform, so that as one surveys the area, the patches of *Mytilus* interspersed among the *Balanus* provide a kind of relief map of the flat.

On this flat also there are a few shallow tide pools, eighteen inches or two feet deep, which contain *Cribrina xanthogrammica, Katharina tunicata, Mopalia muscosa,* and *Strongylocentrotus drobachiensis,* showing that species normally having their distribution in the lower intertidal or demersal zones can subsist at higher levels if the situation is such that they are kept constantly submerged.

A comparable situation obtains on the "flat" on the west side of Waadah Island, which is flat only by contrast with the steepness of much of the island.

Fig. 8. Base of Seal Rock, south side. At the upper left is a point of the adjacent mainland, with Waadah Island showing faintly in the distance. 1. *Ralfsia verrucosa.* 2. *Balanus glandula,* with some *Gigartina* interspersed. 3. *Gigartina papillata* and *Fucus furcatus.* 4. *Mytilus californianus.* 5. *Halosaccion glandiforme.* 6. *Alaria tenuifolia.* 7. *Lessoniopsis littoralis.* The dominants only are listed. In all cases other species are intermingled.

The area consists of a substrate of horizontal or gently sloping rock overlain with large boulders, the tops of which are awash at high tide. The rough and irregular nature of the terrain, with tide-pools at various levels containing characteristic demersal forms, tends to obscure the vertical stratification of organisms so prominent at the other localities studied.

The relative poverty of marine algae on this side of the island has already been noted (p. 338 and Table I). The invertebrate fauna is likewise rather disappointing when one considers the size of the area exposed at low tide. Thirty-three species were collected here, twenty-eight of which occurred at one or more of the other stations. The five species which in our collecting were found only on the Waadah flat are *Acmaea persona, Crepidula adunca, Crepidula nummeria, Epitonium wroblewskii,* and *Tegula funebralis.* Their presence here is presumably correlated with the relatively sheltered conditions, the surf having its force broken as the incoming waves stream among the boulders.

On August 4, 1948, Waadah Island was revisited by one of us (Miller) to ascertain whether any substantial changes in the biological situation had occurred as a result of the erection of a breakwater (shown as a double dotted line in the map, fig. 1) between Waadah Island and the adjacent mainland south of Koitlah Point. This breakwater, about 2800 yards long, was constructed over a two-year period, 1942-43. It is composed of over one million tons of large rocks somewhat irregularly piled together, forming an extremely rough substrate, over which one can scramble only with considerable difficulty. It shelters the harbor from northerly storms.

The breakwater itself provides material for an interesting biological study. Its outer (northerly) face has rapidly been colonized by *Mytilus californianus, Mitella polymerus,* and other characteristic inhabitants of surf-beaten rocks. No *Postelsia* was observed. The inner, sheltered face of the breakwater has developed the usual complement of sessile organisms found in quiet waters, *Balanus glandula, Mytilus edulis, Pisaster ochraceus* being abundant (*B. glandula* and *P. ochraceus* of course occur on the outer face of the breakwater as well.)

So far as could be determined by a quick survey (the breakwater itself and a mile or more of adjacent rocky shore were traversed at one low tide), the zonation of organisms on the breakwater represents simply an extension of that found generally in the vicinity. An unexpected feature was an extraordinary abundance of the twenty-rayed starfish (*Pycnopodia helianthoides*) in the demersal zone on the inner, sheltered face of the breakwater. It was possible to observe one of these every thirty or forty feet over a distance of more than a mile.

The breakwater had exercised no discernible effect on the organisms at the localities described earlier in this paper. At Postelsia Point, which is on the opposite side of Waadah Island from the breakwater, the stand of *Postelsia palmaeformis* in 1948 was thinner than that observed in earlier years, and the individual plants appeared less vigorous. No reason for this was apparent in the physical environment.

General Considerations

The conditions mentioned in the second paragraph of this paper seem to favor an abundant growth of algae. None of the species mentioned, however, are peculiar to the Neah Bay region. It is their great abundance here both as to species and individuals that is impressive, and the same is true of the Port Renfrew region on Vancouver Island.

While a good deal of attention has been given to the form and structure of the large kelps in relation to the factors that determine their distribution (literature cited above) there seems to have been relatively little consideration of the red and the green algae from this point of view. A review of the known facts about the form and structure of the algae of the Neah Bay region in relation to the environmental factors and a further study of the ecological anatomy is highly desirable.

A study of the algae of this region from the viewpoint of the relation between their methods of reproduction and their local distribution would be an interesting line of investigation. Such questions as whether the species is annual or perennial and whether it is reproduced mainly by vegetative means or by spores would add much to our understanding of the biology of the littoral zone in the Neah Bay region. Studies of the winter condition of algae such as have been made by Hurd (1917) for the Puget Sound region or of the seasonal development of species such as have been made by Rigg for Nereocystis (1917) would be interesting work, full of adventure. Wind and rain are common in the region during the winter months and the days are relatively short in this latitude. There are plenty of low tides in the region in winter but they mostly occur between 5 and 9 p.m. Hardy, sure-footed workers experienced in negotiating treacherous waters and provided with good artificial lights could have an adventurous time working on these shores in winter and could contribute valuable data.

Desiccation does not seem to be as important a factor in the zonation of algae here as it probably is in regions where higher temperatures, greater light intensities, and drier winds prevail on the beaches at low tide (cf. Muenscher, 1915). The exposed rocks in the Neah Bay region are usually cold and damp, and the air is the same. Cloudy or foggy weather is more common than bright sunshine especially on early summer mornings when the low tides occur. Many of the algae (e.g. *Polysiphonia* spp. and *Gigartina leptorynchos)* plaster themselves to the surface of the rocks when the tide recedes and retain water among their densely crowded filaments or their numerous proliferations so that they are in little danger of excessive water loss. The distal portions of the larger brown algae form thick layers on the rocks at low tide and are thus likewise protected from excessive loss of water. The smaller red algae in the littoral zone are commonly so completely covered at low tide by the dense layer of brown algae that they are found only by moving their protectors aside. This is notably the case on the south side of Seal Rock. The red algae are thus protected from the effects of desiccation and intense light.

Evidently all the algal associations of the region are climax vegetation. No evidence of succession was found and this seems to be the natural situation for marine algae. Their "soil" is not the rocks to which they attach themselves, but rather the water which bathes them. Their holdfasts are not comparable to the roots of higher plants except in the one function of anchorage. There does not seem to be any evidence that absorption of either water or salts takes place to a greater extent in the holdfast than in other portions of the plant, and no evidence has been found of the storage of food in the holdfasts. The holdfast is not a region of active growth after the plants attain firm anchorage on the surface of the rocks. The boundaries between zones of algae on these shores are sometimes rather sharp but more frequently are seen to be indefinite when carefully studied. In no case are they to be regarded as real tension lines, but rather as an indication that the plants have established themselves where the conditions are suitable for their form, structure, and methods of reproduction. It does not seem probable that their zonation would show successive changes with the passage of years.

The interrelations between the plants and animals of the upper littoral have been a subject of considerable interest to the writers during the course of this survey, but opportunities for the kind of investigation needed have been extremely limited. The sponge *Haliclonia cinereus* seems to flourish especially on the stalks of large algae, and various species of hydroids and Bryozoa grow on the stalks or stipes. The limpet *Acmaea instabilis* has been found nowhere except on the stalks of *Lessoniopsis*. A good many lower intertidal and demersal animals must obtain from the large algae a great deal of protection from the surf, and from desiccation when the tide is out. Algae and algal detritus undoubtedly provide an important, if not indeed the major, source of food in the littoral economy.

It has been stated by Shelford (1930) that, in areas studied by him, plants are to be classed as sub-dominants in both the intertidal and sub-tidal areas. This probably varies from place to place. In the areas under consideration here, plants are sub-dominant in the upper intertidal (figs. 4 and 8), but it is hard to avoid the belief that they should be classed as dominants in the lower intertidal and in at least the proximal part of the demersal zone (figs. 3 and 8).

In the upper intertidal there appears to be competition between plants and animals for "standing room." On the whole the animals seem to be more successful in occupying the available space. In a situation such as that shown in figure 8, the impression is almost inescapable that the algae have been crowded out to the very borders of the colonies of *Balanus* and *Mytilus*. On the other hand, one finds instances where the algae seem to have gained additional anchorage by pushing their holdfasts in among the barnacles.

Plants and animals struggle endlessly for existence in the rigorous environment of a surf-swept shore. The micro-ecology of these wave-beaten communities presents fascinating possibilities for further study.

Summary and Conclusions

A survey is here reported of the vertical distribution of a number of species of marine algae and marine invertebrates in or adjacent to the intertidal zone at certain localities in the vicinity of Neah Bay in the extreme northwest corner of the continental United States.

Steep rocky shores, considerable surf, a large tidal range, and a moist climate free from extremes of temperature, form an environmental complex favorable to an abundant intertidal flora and fauna. At different vertical levels, different species are dominant, resulting in a zonation of organisms so distinct as to be visible in the form of conspicuous horizontal bands.

For selected localities, tabulations have been made of the vertical range, in feet above or below zero tide datum, of the principal species of brown, red, and green algae, and of the vertical distribution of a number of littoral invertebrates in zones, as follows: (A) splash zone; (B) upper intertidal; (C) lower intertidal; (D) demersal.

At a typical locality ("Postelsia Point" on Waadah Island) eight zones of algae are clearly distinguished. These are in order from top to bottom: (1) Ralfsia-Prasiola, (2) Endocladia-Gigartina, (3) Postelsia, (4) Halosaccion, (5) Alaria, (6) Lessoniopsis, (7) Laminaria, and (8) Nereocystis.

Only above the large algae is the zonation of invertebrates conspicuous. In the upper intertidal belt we find a large stand of *Mytilus californianus* intermingled with *Endocladia, Gigartina*, and—on points most exposed to the surf—dense colonies of *Mitella polymerus*. Above these, but still in the upper intertidal, occurs a nearly pure stand of *Balanus glandula*. Still, above this, in the splash zone, we find a belt of *Littorina sitchana* and *Acmaea digitalis* with scattered *Balanus glandula*.

On a similar rocky shore which slopes more gently (south side of Seal Rock), the width of these bands of organisms increases, in inverse proportion to the steepness of the slope, emphasizing the significance of vertical range. On a wide wave-cut bench at a suitable level (east end of Seal Rock), *Balanus* *glandula* forms a dense growth over an area as large as a city lot, although on a vertical shore the width of the belt in which this organism would be similarly dominant would hardly exceed ten inches.

At levels below the upper intertidal, zonation of animal life is less conspicuous because of the abundance of algae, which the present authors class as dominants in the lower intertidal and at least the proximal part of the demersal zone.

Zonation is regarded as a resultant of two primary factors, which are in fact reciprocals of each other: (A) Organisms of the upper littoral have an optimum vertical range that is determined by a variety of conditions, among which are food supply; illumination; degree of resistance to desiccation when exposed to air and sunshine, and to endosmosis when exposed to rain; and adaptability to survival under the pounding of heavy surf. (B) Organisms characteristic of a given vertical range often can and do survive in limited numbers above or below the level regarded as optimum. It would appear that such organisms could, in the absence of competition, successfully occupy much wider vertical ranges. Their apparent restriction to a narrow belt is due primarily to competition from other organisms better adapted to the vertical ranges immediately adjacent.

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[Note.—The authors have cited only literature relating to the area under discussion. For a more general bibliography cf. Hewitt (1937) and Dakin, *et al.*, (1948), which are included below.]

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